# Late-Wisconsin and Holocene Vegetation in Arches National Park, Utah

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Abstract. Eleven *Neotoma* spp. (packrat) middens, dating from approximately 20,000 B.P. to the present, were collected from a single alcove site at 1,317 m elevation in Arches National Park, Grand County, Utah. Macroscopic plant remains from these late-Wisconsin and Holocene middens generally support other records of elevational displacements for plants on the Colorado Plateau. Results indicate that vegetation more mesophytic than present dominated the Bison Alcove area between 20,000 and 12,500 B.P. *Pinus flexilis* (limber pine) and *Pseudotsuga menziesii* (Douglas-fir), no longer growing in the park, predominate the fossil assemblages. A minimum Pleistocene displacement of 513 m for *Pinus flexilis* and 208 m for *Pseudotsuga menziesii* is indicated. Modern vegetation was in place at this location sometime before 2.660 B.P.

**Key words:** Arches National Park, Holocene vegetation, late-Wisconsin vegetation, packrat midden, paleoecology, Pleistocene vegetation.

Analyses of packrat middens contribute valuable data to the late-Quaternary record of the southwestern United States. Packrat middens help define local vegetation chronologies and migrational patterns within the Chihuahuan, Sonoran, Mojave, Great Basin, and Colorado Plateau deserts during the last 40,000 years (Betancourt et al. 1990). Fossil middens can contain abundant local biotic information; plants, bones, and fecal material from various animals are all collected by packrats from within 30–50 m of their nests (Stones and Hayward 1968; Finley 1990). These preserved remains provide excellent data for the reconstruction of local floral and faunal communities.

Documenting vegetation during the full-glacial regime of the Wisconsin and the change to the more xerophytic vegetation of today is possible by analysis of packrat middens. Information is available also concerning the timing of vegetation change, community composition, and individual species' latitudinal and elevational migration. Vegetation chronologies from areas to the south and west of Arches National Park (ANP) have been compiled by Betancourt (1984, 1990), Spaulding and Petersen (1980), Davis et al. (1984), and Mead et al. (1987).

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This research adds to that record by reconstructing the late-Wisconsin and late-Holocene floral communities in ANP. Two main questions are addressed:

- 1. How much and when were subalpine floral species elevationally displaced in ANP during the late-Wisconsin interval?
- 2. How do these data support or contradict other paleoenvironmental models in adjacent areas?

Relative to the first question, certain plants inhabited lower elevations during the terminal Wisconsin glacial advance and migrated to new locations during the Holocene warming trend. Displacement values of fossil taxa are determined through comparison with the elevational and latitudinal distribution of modern species. Species arrivals and departures from the midden record are also noted. This information will be used to track community change over time by determining community composition and an individual taxon's response to climatic change—both spatially and temporally. The data are useful in light of projected global warming because of increased CO<sub>2</sub> and other trace gases in the atmosphere. A doubling of CO<sub>2</sub> will increase average global temperatures from 1.9 to 5.2°C. This projected rate of change will be equal to or greater than the greatest rate that occurred during Pleistocene deglaciations (Crowley and North 1991).

Question two will be approached by comparing packrat midden and paleovegetation research in adjacent areas including localities in Utah (Fishmouth and Allen Canyon caves [Betancourt 1984], Natural Bridges National Monument [Mead et al. 1987], Cowboy Cave [Spaulding and Petersen 1980], and Bechan Cave [Davis et al. 1984]) and Colorado (La Plata Mountains [Petersen 1988]). This information will increase the resolution of past vegetation and climate on the Colorado Plateau.

# **Physiographical Setting**

Arches National Park, located approximately 8 km north of Moab, Utah, contains 297 km². The park is composed primarily of 135–195 million-year-old Jurassic age sandstones (Baars 1983) forming bedrock expanses, cliffs, arches, and spires. Perennial running water is not abundant, although the Colorado River delineates Arches' south–southeastern boundary. Seeps and springs are visible at various contact points within the Entrada or Navajo Sandstone formations, and a few intermittent streams flow within the park.

The climate of southeastern Utah is arid with hot, dry summers and cool to cold winters. Based on 83- and 94-year temperature and precipitation records in Moab (1,220 m elevation), the annual average temperature is 12.9°C, and precipitation averages 21.6 cm annually (U.S. Weather Bureau,

summary of the climatological data for the United States by sections, section 10, eastern Utah). Most precipitation falls between August and October.

The midden collection site is located in the southeastern portion of the park. It is informally named Bison Alcove because of the skeletal elements of *Bison bison* found within the shelter. Bison Alcove faces south at an elevation of 1,317 m. It is formed at the contact between the Dewey Bridge member (also called the Carmel Formation) and the Slick Rock member of the Entrada Formation. The entrance is approximately 10 m high and 22 m wide. The back wall of the alcove is approximately 13 m from the drip line. The floor is steep and choked with large boulders. Abundant packrat midden deposits are located throughout.

A large sand dune covered by a sparse pinyon–juniper community is immediately outside the shelter. A small, dense stand of Gambel oak (*Quercus gambelii*) is approximately 13 m from the drip line. Ground cover, calculated at 49%, includes cacti, graminoids, and herbaceous and woody-herbaceous plants.

### Methods

Eleven of 20 midden samples removed from Bison Alcove were analyzed. Middens were scraped to remove the outer rind, disaggregated in distilled water for approximately 5 days, washed through a 20-mesh (0.84-mm) soil screen, and air dried (as in Van Devender 1973). Remains were hand-sorted and identified to the lowest taxonomic level possible by matching with herbarium collections. Individual taxa were recorded as 1 = rare (1–2 fragments), 2 = uncommon (3–10 fragments), 3 = common (11–50 fragments), 4 = very common (51–100 fragments), and 5 = abundant (>100 fragments), following methods developed by Van Devender (1973).

Eleven midden assemblages were radiometrically dated by Beta Analytic, Inc., using representative specimens from each midden (Table 1). Two components from midden BA-2 were dated: Pseudotsuga menziesii needles and dung from Neotoma spp. The divergent dates of 13,140 ± 380 B.P. (Pseudotsuga menziesii) and 14,910 ± 100 B.P. (Neotoma spp.) do not overlap at three standard deviations. It is possible that older packrat dung could have been incorporated into the nest before it was indurated, that a sample was inadvertently chosen containing overlapping middens, or that some other error occurred during the process of sorting or dating the middens. For these reasons, the Pseudotsuga menziesii date of 13,140 ± 380 B.P. was chosen to represent this assemblage (after the method of Long and Rippeteau 1974). A recent unindurated midden containing green floral material was collected from the rear surface of the alcove. Faunal elements of Bison bison (bison) and Ovis canadensis (bighorn sheep) were also contained within this assemblage. These keratin hoof and horn elements dated to  $355 \pm 60$  and  $405 \pm 60$  B.P.

Table 1. Radiocarbon dates from Bison Alcove, Arches National Park, Utah.

Sample	14-C B.P.	Laboratory <sup>a</sup> number	Material dated
Modern	405 ± 60	32293	Keratin: hoof and horn
	$355 \pm 60$	32292	
BA-07a	$1,860 \pm 70$	38335	Neotoma spp. dung
BA-05	$1,930 \pm 80$	31318	Juniperus needles
BA-10	$2,660 \pm 60$	38336	Neotoma spp. dung
BA-01	$12,420 \pm 210$	31313	Pinus flexilis needles
BA-02	$13,140 \pm 380$	31314	Pseudotsuga needles
BA-02	$14,910 \pm 100$	31315	Neotoma spp. dung
BA-12	$15,250 \pm 100$	38747	Neotoma spp. dung
BA-04	$15,270 \pm 230$	31317	Neotoma spp. dung
BA-03	$16,460 \pm 170$	31316	Neotoma spp. dung
BA-15	$16,530 \pm 100$	38748	Neotoma spp. dung
BA-13	$20,050 \pm 160$	38337	Neotoma spp. dung

a Beta Analytic, Inc.

Two vegetation transects, taken 23 May 1990, provided modern data for comparison (Table 2). Percent ground cover of each species was calculated. Plants in the immediate area, but not along the transects, were also noted.

#### **Results and Discussion**

The radiocarbon dates on middens from Bison Alcove are not evenly distributed in time. Though a concerted effort was made to identify mid-Holocene middens, a gap of 9,760 years is found in the record at Bison

Table 2. Modern vegetation found at Bison Alcove, Arches National Park, Utah.

Species <sup>a</sup>	Percent cover of total vegetation <sup>b</sup>	Found in modern midden
Bromus tectorum	6	Poaceae
Cryptantha crassisepala	3	Cryptantha sp.
Cryptantha flava	3	Cryptantha sp.
Ephedra viridis	14	
Hymenopappus filifolius	en contain 1 overlapping	Asteraceae
Quercus gambelii	23	
Rumex hymenosepalus	LEL To stab 1 stranger by	
Sporobolus contractus	5	Poaceae
Sporobolus cryptandrus	22	Poaceae
Stipa hymenoides	of the slowed Lynnia sets to	Poaceae
Vanclevea stylosa	18	Asteraceae

<sup>&</sup>lt;sup>a</sup> Additional species observed nearby but not on transect: Asclepias cryptoceras, Ceratoides lanata, Coleogyne ramosissima, Juniperus osteosperma, Lepidium sp., Machaeranthera canescens, Mentzelia sp., Opuntia polyacantha, and Pinus edulis.

b Percent vegetation is 49; percent sand is 51.

Alcove (from 12,420 to 2,660 B.P.). When frequency distributions are plotted for more than 1,000 middens collected and dated throughout the southwest (Webb and Betancourt 1990), a decline in middens dating between 4,000 and 8,000 years ago is evident in the Chihuahuan, Sonoran, Mojave, Great Basin and the Colorado Plateau deserts. Webb and Betancourt (1990) state that there may be "a physical cause . . . but a single cause is unlikely for the entire western United States, given such a wide range of climatic and physiographic conditions." This gap is presently unexplained.

Macrofossil analysis to the lowest taxonomic level possible resulted in 270 identifications from 27 plant families. These 11 midden assemblages represent three different periods: full-glacial (22,000-14,000 B.P.), late-glacial (14,000-11,000 B.P.), and late-Holocene (4,000-present; as in Van Devender et al. 1987). The number of genera identified in each dated midden varies from 14 to 25.

#### Late-Wisconsin

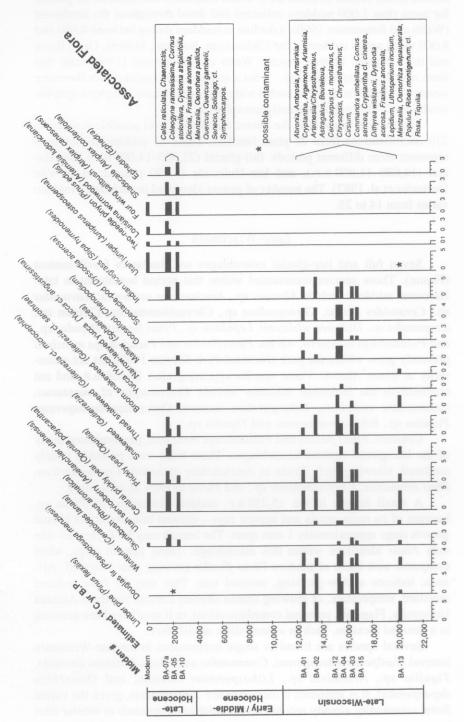
Seven full and late-glacial assemblages are similar in fossil content (Figure). Those species represented within this period but absent in late-Holocene middens include Abronia sp., Amelanchier utahensis, Astragalus sp., Ceratoides lanata, Chenopodium sp., Chrysothamnus sp., Cirsium sp., Cryptantha sp., Dithyrea wislizenii, Lepidium sp., Pinus flexilis, Populus sp., and Pseudotsuga menziesii. All but Pinus flexilis and Pseudotsuga menziesii presently grow within the park (National Park Service 1987) but not necessarily at Bison Alcove. Those species appearing after 20,050 B.P. and not recorded in the Holocene middens include Cercocarpus cf. montanus, Commandra umbellata, Lithospermum incisum, Osmorhiza depauperata, Populus sp., Ribes montigenum, and Tiquilia sp.

Conifers, Pinus flexilis and Pseudotsuga menziesii, predominated many of the late-glacial midden assemblages. These trees were probably widely scattered, allowing such shrubs as Amelanchier utahensis, Cornus sericea, Rhus aromatica, Chrysothamnus sp., and Yucca to grow as understory.

A small branch in the 15,250 B.P. midden—identified as Pinus sp. because of its resin canals and narrow rays—showed thin, indistinct annual growth rings approximately 1 mm apart. The branch may be P. flexilis—the only Pinus identified within this assemblage. These growth rings, when compared with those of modern Pinus flexilis growing near Flagstaff, Arizona, indicate a slow-growing, stressed tree. This may be from reduced moisture, temperature, or growing season (Robert Larson, Northern Arizona University, Flagstaff, personal communication), or it may have been growing in a stressed location, such as a steep slope or cliff face.

Several species are found as single occurrences in the late-Wisconsin interval (Juniperus osteosperma, Commandra umbellata, Fraxinus anomala, Tiquilia sp., Artemisia sp., Lithospermum incisum, and Osmorhiza depauperata). It is unknown if these taxa are contaminants, given the varied floral community already reconstructed. Additional research at similar sites

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Arches National Park, Utah Figure. Chronosequence of selected plant macrofossils and their relative abundances from Bison Alcove,

on the Colorado Plateau is needed so that these occurrences can be verified. Taxa that occur during both the late-Wisconsin and Holocene periods are Cornus sericea, Gutierrezia spp., Mentzelia sp., Opuntia polyacantha, Rhus aromatica, Sphaeralcea sp., Stipa hymenoides, and Yucca sp.

The most likely contaminant is Juniperus osteosperma, from a midden dated at 20,050 B.P. and represented by a twig 0.7 mm long. This taxon has been reported from 30,000-year-old packrat middens from similar sites in upper Salt Creek in Canyonlands National Park (J. I. Mead, Northern Arizona University, Flagstaff, personal communication). It is possible that this species persisted at Bison Alcove into the Wisconsin glacial period or it could be a contaminant from an older midden. Juniperus osteosperma then disappears from the Arches record until the Holocene, where it is found in all the late-Holocene middens. It presently grows in elevations between 850 and 2,135 m (Welsh et al. 1987). Pseudotsuga menziesii presently grows at 1,525–3,050 m, and Pinus flexilis grows at 1,830-3,450 m, so the co-occurrence of these three species during the late Pleistocene is not impossible. A mass spectrometer date on the juniper twig would specify its true age.

Juniperus scopulorum (Rocky Mountain juniper) has been recovered from many Pleistocene-age middens throughout the Colorado Plateau. Reports from Falling Arch (1,460 m) and Fishmouth Cave (1,585 m) show J. scopulorum dropping from the record by 9,200 and 9,700 B.P., respectively (Betancourt 1990). This taxon was not found in any of the Bison Alcove middens—it may not have grown as low as 1,300 m during the late Pleistocene.

Many of the full- and late-glacial taxa recorded at Bison Alcove are also found at Bechan Cave (Davis et al. 1984), 1,280 m in elevation. Fossil plant remains recovered from the dung layer dating 12,900–11,700 B.P. indicate a similar late-glacial community. Species shared by both sites include: Amelanchier sp., Atriplex cf. canescens, Chenopodium sp., Cirsium sp., Cornus sericea, Opuntia polyacantha, Ribes sp., Rosa sp., Sphaeralcea sp., and Stipa hymenoides.

Late-Wisconsin taxa identified at Bison Alcove are also recorded in a stratigraphic layer dating approximately 8,700 B.P. (elevation 1,770 m) at Cowboy Cave (Jennings 1980). Taxa in common include Amelanchier utahensis, Chenopodium sp., Cornus sericea, Fraxinus anomala, Opuntia sp., Populus sp., Pseudotsuga menziesii, Rhus aromatica, Rosa woodsii, Stipa hymenoides, and Yucca sp. (Albee 1980:195). Picea sp., found at Cowboy and Bechan caves, was not recovered from any of the Bison Alcove middens.

Other late-Wisconsin macroscopic plant remains found at nearby locations agreeing with the Bison Alcove record include Rosa sp. and Artemisia sp. at 1,820 m (Mead et al. 1986) and Rhus aromatica and Fraxinus anomala recovered from approximately 1,200 m (Withers 1989). At Fishmouth Cave, elevation 1,585 m, late-glacial middens analyzed by Betancourt (1984) included Cornus sp., Ribes sp., and Yucca angustissima. Their presence helps substantiate the inclusion of these singly-occurring genera in Bison Alcove late-Wisconsin plant assemblages.

Reconstructed plant assemblages from Bison Alcove correspond with other fossil vegetation assemblages from the central Colorado Plateau and show that *Pinus flexilis* and *Pseudotsuga menziesii* inhabited the areas now occupied by pinyon–juniper woodland. Minimum elevational displacements are 513 m for *Pinus flexilis* and 208 m for *Pseudotsuga menziesii*. A cooler and possibly wetter environment during the late-Wisconsin is indicated by the midden assemblages at this site.

#### Late-Holocene

Four middens date from this period. Taxa found exclusively in these late-Holocene assemblages include Artemisia ludoviciana, Atriplex canescens, A. confertifolia, Celtis reticulata, Coleogyne ramossissima, Ephedra sp., Pinus edulis, and Quercus gambelii. All these species presently grow in the park, but only Coleogyne ramosissima, Ephedra sp., Pinus edulis, and Quercus gambelii are found at the site today.

The middens dating from this period indicate that modern vegetation grew at Bison Alcove by 2,660 B.P. Two genera recorded at this date seem to be slightly more mesophytic than modern taxa directly outside the alcove—*Artemisia ludoviciana* and *Cornus sericea*. Petersen (1988) suggests that the La Plata Mountains, Colorado, were cooler and drier than present between 2,800 and 2,500 B.P. with a warming trend beginning around 2,500 B.P.

## **Conclusions**

The analysis of macroscopic plant remains from packrat midden sequences in Arches National Park has produced the following:

- 1. The plant community near Bison Alcove, from approximately 20,000 to 12,500 B.P., was dominated by vegetation reflecting an effectively cooler environment than at present. Two species that no longer grow in the area (*Pinus flexilis* and *Pseudotsuga menziesii*) predominate these fossil assemblages. A minimum elevational displacement of 513 m for *Pinus flexilis* and 208 m for *Pseudotsuga menziesii* is indicated.
- 2. Plants persisting at the site from the late-Wisconsin through the present include *Gutierrezia* sp., *Opuntia polyacantha*, *Rhus aromatica*, *Sphaeralcea* sp., and *Stipa hymenoides*.
- 3. Modern vegetation existed near Bison Alcove by 2,660 B.P. However, the occurrence of *Artemisia ludoviciana* and *Cornus sericea* at that date may suggest more effective moisture than today.

These data generally support other paleoenvironmental reconstructions on the Colorado Plateau. Further research should be conducted to fill the

middle Holocene age gap at Bison Alcove or in other localities in ANP. Also, with additional data from this location, the timing of the Pleistocene–Holocene transition could be ascertained, species arrival times and migration patterns analyzed, and the paleoecology and climatic parameters of the central Colorado Plateau refined.

# **Middens and Future Planning**

Packrat middens are playing an ever-increasing role in paleoenviron-mental reconstruction. They are providing significant information regarding past local and regional vegetational and climatic change that can help us to predict plants' responses to future climatic fluctuation. Middens can also reveal vital information about the expansion and contraction of plant and animal populations, enabling us to deduce changes in these communities so that we can better understand the adaptability of biotic organisms. In these ways, paleovegetation records gathered from packrat middens can help to form the basis for future planning decisions. This report is significant for future park planning in three areas—preservation of the deposits, resource management planning, and regional concerns.

### Preservation of Deposits

Initially, a strategy for the preservation of packrat midden deposits must be formulated. An inventory of middens should be initiated, along with an assessment of their significance.

Four factors can be used to help determine the significance of a midden deposit. Protection from moisture is the first factor. Dry alcove sites and overhanging ledges help preserve middens and their contents. Second, a midden can be examined in situ for extralocal or local vegetation to estimate its age. Conifer needles (Juniperus spp., Picea spp., and Pinus spp.) are readily apparent and can indicate a general age. The ecological community in which a midden is located is also important. Rocky outcrops, grassland, or riparian environments will all host different plant taxa available for collection by the packrat. Fossil midden assemblages located in different communities will provide data regarding specific environments. Finally, in general, the more numerous the middens in an area, the better the potential vegetation record over time. For example, an alcove containing different midden assemblages or a canyon with many individual midden sites can provide more potential information than one isolated midden. Also, sites such as Bison Alcove, which contain both raptor roosts and middens, can provide a unique paleoenvironmental record of datable vegetational and faunal communities.

Fossil middens that are threatened by natural hazards or visitor traffic should be stabilized or collected. Once significant midden locations are documented, these areas should have the same protection accorded to archaeological sites.

## Resource Management Planning

Packrat midden research can also contribute to specific resource management decisions. Contributions to issues regarding geographical range expansion and contraction, population dynamics and species diversity, and composition of pre-Columbian communities are possible through packrat midden paleovegetation studies.

Studies should be initiated to determine which plants and animals inhabited national parks over time to determine local extinction and dispersal in relation to climatic variation. If disappearances and migrations can be reliably documented, insights can also be gained on geographic expansion and contractions. If a decrease in such species as juniper can be documented in the past, cause(s) for their present decline may be more easily understood. Also, factors influencing rare and endangered plant populations may be more easily ascertained.

### Regional Planning Concerns

Paleoecological reconstruction using packrat middens can also augment land use decisions on a regional scale. Data from middens make it clear that plant communities, and therefore animal populations, are not static and will continue to change over time, although we do not yet have enough information to predict how they will change. With the potential consequences of increased  $\mathrm{CO}_2$  in our atmosphere (global warming), plant and animal communities are likely to be greatly affected.

The degree and rate of warming in the next 100 years is estimated to at least equal the degree and rate of warming experienced at the Pleistocene–Holocene transition (Crowley and North 1991). The analysis of fossil midden contents during this transition period can provide valuable information regarding biotic change resulting from climatic variation at a similar magnitude.

Also, taxa recovered from middens dating during the mid-Holocene warm period (4,000–8,000 B.P.) may provide another analog to the global warming we may soon experience. It is already known that oak and ponderosa pine increased their ranges during that time. Further analysis of midden contents dating from these critical periods can provide greater resolution on how climate change affects individual taxa and communities.

Plants either persist, become locally extinct, or migrate to more favorable areas when the climate changes and habitats degrade (Thompson 1988). As species die in the more marginal areas of their ranges, we face a tremendous loss of species diversity (Davis 1989). Studies on migration rates based on paleoecological reconstructions indicate that certain plants may not be able to migrate fast enough to keep up with climatic warming (Davis 1989; Gear and Huntley 1991). Therefore, large areas of diverse habitats and routes

or corridors should be set aside and federally protected so that plants and animals can more easily disperse to favorable locations.

Federal and state lands on the Colorado Plateau have the potential to be designated by legislation as special influx areas and migration routes. The Green and Colorado river corridors could provide routes to higher or lower elevations as many portions of these river corridors are already protected by federal legislation. Because the topography and moisture vary substantially throughout the Plateau, suitable public land areas are available in diverse microenvironments to provide niches for migrating species. These areas should be utilized to manage and preserve the diverse ecosystems that we enjoy today.

#### Future Research

Extraction of DNA and stable isotope analyses applied to ancient packrat midden materials are providing new information on mechanisms of plant response to past climate change through genotypic variation and varying plant physiological response. Increased resolution of drought severity, growing season temperature, and effective precipitation are now possible using these techniques.

Fingerprinting of DNA using polymerase chain reaction can determine genotypic variation within modern species (Arnheim et al. 1990; Neale and Williams 1990; Strauss and Doerksen 1990). By using techniques of recombinant DNA, genetic material can be extracted from plant materials within middens so that fossil and modern genetics can be compared (Rogers and Bendich 1985). Thus, change in genetic variation over time can be determined and considered when modeling past migration patterns and as a mechanism for responding to changing climatic regimes.

Isotopic ratios of hydrogen and oxygen in plant tissues can provide information on temperature and effective penetration of rainfall into continental interiors (Dansgaard 1964). Carbon isotopic ratios provide information on water use efficiency and the growth success of plants (Farquhar and Richards 1984; Toft et al. 1989; Ehleringer et al. 1990). Deuterium values, extracted from modern and fossil material, are sensitive to growing season temperatures (Long et al. 1990). Modern values of these indices can be compared with values from fossil plants in middens so that change in past temperature, precipitation, and hydrologic cycles can be further refined.

Packrat middens are truly repositories of the past. This recent research is focusing on immediate and sensitive plant response to climatic change through individual plants' ecophysiologies rather than general plant responses at the community level. As new scientific techniques become available, midden research will be able to provide even greater resolution regarding past biotic systems and climatic regimes.

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## **Literature Cited**

- Albee, B. J. 1980. Macrofossils identified from first bulk sample of leaf layer, stratum IIa. Pages 193-194 in J. Jennings, editor. Cowboy Cave. University of Utah Press, Salt Lake City.
- Arnheim, N., T. White, and W. E. Rainey. 1990. Application of PCR: organismal and population biology. BioScience 40:174-182.
- Baars, D. L. 1983. The Colorado Plateau. University of New Mexico Press, Albuquerque. 279 pp.
- Betancourt, J. L. 1984. Late Quaternary plant zonation and climate in southeastern Utah. Great Basin Naturalist 44:1-35.
- Betancourt, J. L. 1990. Late Quaternary biogeography of the Colorado Plateau. Pages 259-292 in J. L. Betancourt, T. R. Van Devender, and P. S. Martin, editors. Packrat middens: the last 40,000 years of biotic change. University of Arizona Press. Tucson.
- Betancourt, J. L., T. R. Van Devender, and P. S. Martin, editors. 1990. Packrat middens: the last 40,000 years of biotic change. University of Arizona Press, Tucson, 472 pp.
- Crowley, T. C., and G. R. North. 1991. Paleoclimatology. Oxford University Press, New York. 339 pp.
- Dansgard, W. 1964. Stable isotopes in precipitation. Tellus 16:436-468.
- Davis, M. B. 1989. Lags in vegetation response to greenhouse warming. Climatic Change 15:75-82.
- Davis, O. K., L. D. Agenbroad, P. S. Martin, and J. I. Mead. 1984. The Pleistocene dung blanket of Bechan Cave, Utah. Pages 267-282 in Contributions in Quaternary vertebrate paleontology. Carnegie Museum of Natural History Special Publication 8. Washington, D.C.
- Ehleringer, J. R., J. W. White, D. A. Johnson, and M. Brick. 1990. Carbon isotope discrimination, photosynthetic gas exchange, and transpiration efficiency in beans and range grasses. Acta Oecologica 11:611-625.
- Farquhar, G. D., and R. A. Richards. 1984. Isotopic composition of plant carbon correlates with water use efficiency of wheat genotypes. Australian Journal of Plant Physiology 11:539-552.
- Finley, R. B. 1990. Woodrat ecology and behavior and the interpretation of paleomiddens. Pages 24-28 in J. L. Betancourt, T. R. Van Devender, and P. S. Martin, editors. Packrat middens: the last 40,000 years of biotic change. University of Arizona Press, Tucson.
- Gear, A. J., and B. Huntley. 1991. Rapid changes in the range limits of Scots pine 4,000 years ago. Science 251:544-547.
- Jennings, J. 1980. Cowboy Cave. University of Utah Anthropological Papers. University of Utah Press, Salt Lake City. 224 pp.
- Long, A., and B. Rippeteau. 1974. Testing contemporaneity and averaging radiocarbon dates. American Antiquity 39:205-215.
- Long, A., L. A. Warneke, J. L. Betancourt, and R. S. Thompson. 1990. Deuterium variations in plant cellulose from fossil packrat middens. Pages 380-396 in

- J. L. Betancourt, T. R. Van Devender, and P. S. Martin, editors. Packrat middens: the last 40,000 years of biotic change. University of Arizona Press, Tucson.
- Mead, J. I., L. D. Agenbroad, O. K. Davis, and P. S. Martin. 1986. Dung of Mammuthus in the arid southwest, North America. Quaternary Research 25:121-127.
- Mead, J. I., L. D. Agenbroad, A. M. Phillips III, and L. T. Middleton. 1987. Extinct mountain goat (Oreamnos harringtoni) in southeastern Utah. Quaternary Research 27:323-331.
- National Park Service. 1987. Plant list, Arches National Park. Canyonlands Natural History Association, Moab, Utah. 8 pp.
- Neale, D. B., and C. G. Williams. 1990. Restriction fragment length polymorphism mapping in conifers and applications to forest genetics and tree improvement, Canadian Journal of Forest Research 21:545-554.
- Petersen, K. L. 1988. Climate of the Dolores River Anasazi. University of Utah Anthropological Papers 113. University of Utah Press, Salt Lake City. 152 pp.
- Rogers, S. O., and A. J. Bendich. 1985. Extraction of DNA from milligram amounts of fresh, herbarium and mummified plant tissues. Plant Molecular Biology
- Spaulding, W. G., and K. L. Petersen. 1980. Late Pleistocene and early Holocene paleoecology of Cowboy Cave. Pages 163-177 in J. Jennings, editor. Cowboy Cave. University of Utah Press, Salt Lake City.
- Stones, R. C., and C. L. Hayward. 1968. Natural history of the desert woodrat, Neotoma lepida. American Midland Naturalist 80:458–476.
- Strauss, S. H., and A. H. Doerksen. 1990. Restriction fragment analysis of pine phylogeny. Evolution 44:1081-1096.
- Thompson, R. S. 1988. Vegetation dynamics in the western United States; modes of response to climatic fluctuations. Pages 415-458 in B. Huntley and T. Webb III, editors. Vegetation history. Kluwer Academic Publishers. Dordrecht, The Netherlands.
- Toft, N. L., J. E. Anderson, and R. S. Nowak. 1989. Water use efficiency and carbon isotope composition of plants in a cold desert environment. Oecologia 80:11-18.
- Van Devender, T. R. 1973. Late Pleistocene plants and animals of the Sonoran Desert: a survey of ancient packrats in southwestern Arizona. Ph.D. dissertation. University of Arizona, Tucson. 199 pp.
- Van Devender, T. R., R. S. Thompson, and J. L. Betancourt. 1987. Vegetation history of the deserts of southwestern North America: the nature and timing of the late Wisconsin-Holocene transition. Pages 323-352 in W. F. Ruddiman and H. E. Wright, Jr., editors. North American and adjacent oceans during the last deglaciation. Geological Society of America, Vol. K-3, Boulder, Colo.
- Webb, R. H., and J. L. Betancourt. 1990. The spatial and temporal distribution of radiocarbon ages from packrat middens. Pages 85-102 in J. L. Betancourt, T. R. Van Devender, and P. S. Martin, editors, Packrat middens; the last 40,000 years of biotic change. University of Arizona Press, Tucson.
- Welsh, S. L., N. D. Atwood, S. Goodrich, and L. C. Higgins. 1987. A Utah flora. Great Basin Naturalist Memoirs 9. Brigham Young University, Provo, Utah. 894 pp.
- Withers, K. 1989. Late Quaternary vegetation and climate of Forty-mile Canyon and Willow Gulch, in the central Colorado Plateau. M.S. thesis, Northern Arizona University, Flagstaff. 71 pp.

#### Appendix Species Identified By Common Name (based on Welsh et al. 1987)

Species	Common name	
Abronia	Verbena	
Amelanchier utahensis	Utah serviceberry	
Artemisia	Sagebrush	
Artemisia ludoviciana	Louisiana wormwood	
Astragalus	Milkvetch	
Atriplex canescens	Four wing saltbush	
Atriplex confertifolia	Shadscale	
Bromus tectorum	Cheatgrass	
Celtis reticulata	Netleaf hackberry	
Ceratoides lanata	Winterfat	
Cercocarpus montanus	Alderleaf mountain mahogany	
Chenopodium	Goosefoot	
	Rabbitbrush	
Chrysothamnus	Thistle	
Cirsium	Blackbrush	
Coleogyne ramosissima		
Commandra umbellata	Bastard toadflax	
Cornus sericea	Red-osier dogwood	
Cryptantha	Cryptantha	
Cryptantha crassisepala	Plains cryptantha	
Cryptantha flava	Yellow cryptantha	
Dithyrea wislizenii	Spectacle-pod	
Ephedra	Ephedra	
Ephedra viridis	Mormon tea	
Fraxinus anomala	Single-leaf ash	
Gutierrezia	Snakeweed	
Hymenopappus filifolius	Hyalineherb	
Juniperus osteosperma	Utah juniper	
Juniperus scopulorum	Rocky Mountain juniper	
Lepidium	Cress	
Lithospermum incisum	Showy stoneseed	
Mentzelia	Stickleaf	
Opuntia polyacantha	Central prickly pear	
Osmorhiza depauperata	Sweet-cicely	
Picea	Spruce	
Pinus edulis	Two-needle pinyon	
Pinus flexilis	Limber pine	
Populus	Poplar	
Pseudotsuga menziesii	Douglas-fir	
Quercus gambelii	Gambel oak	
Rhus aromatica	Skunkbush	
Ribes montigenum	Gooseberry currant	
Rosa woodsii	Woods rose	
Rumex hymenosepalus	C	
Sphaeralcea	M-11	
Sporobolus contractus	Spike dropseed	
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Sporobolus cryptandrus	Sand dropseed	
Stipa hymenoides	Indian ricegrass	
Tiquilia	Daginbugh	
Vanclevea stylosa	Resinbush	
Yucca angustissima	Narrow-leaved yucca	